A DECADE OF SEX LIFE OF PLANTS

A Report by Plant Reproductive Ecology Group

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WBC
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A DECADE OF SEX LIFE OF PLANTS

** Bees do it*
Birds do it
In Bangalore
Even beans do it.

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* Modified from Nakamura, R.R.(1990) Plant kin selection. Evol. Theory, 5:113-117

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1. INTRODUCTION

1. INTRODUCTION

Last few decades saw more ecologists and evolutionists entering the area of plant reproductive biology because of its potentiality in offering a wide range of systems to test the newly emerging conceptual issues. Consequently more meticulous and innovative investigations were taken up which brought to light more intriguing strategies and patterns of plant reproduction. We, at the University of Agricultural Sciences, Bangalore, started our work on Plant Reproductive Ecology when this 'rush' in the area had just started. From 1980 to 1990, we have grown up as a small working group. This booklet is aimed at summarising the range of issues addressed and the systems investigated at our unit.

Our working methodology has been to look around for patterns, raise questions and try to explain them using the existing hypotheses. Often however when we failed to explain the observed patterns using the treaded paths, we were prompted to explore other conceptual bases. Consequently, our work has opened up new areas of investigations in plant reproductive ecology. Clearly, our methodology of working has paid rich dividends and we wish to pursue the same way.

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2. THE TEAM

2. THE TEAM

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3. SUMMARY OF THE WORK DONE

3.1 SIBLING RIVALRY AND PARENT OFFSPRING CONFLICT IN PLANTS

Trivers (1974) noticed that in several species, parents and their offspring exhibit conflict in different ways. For instance when he was in India during 1972, he noticed dramatic cases of such conflict in langurs and baboons during the weaning period. Typically, towards the end of the weaning period, the mother would tend to neglect the young while the latter beg milk by uttering piercing cries and may even retaliate fiercely when rebuffed by the mother. Mothers are forced to concede to the demands by the infants; otherwise the infant calls may attract the predators threatening the safety of the whole family. Based on these observations Trivers (1974) proposed the concept of parent-offspring conflict (POC).

POC implies that while parents are selected to invest resources equally among all the offspring, the latter would be selected to demand more in order to increase their own individual fitness. Thus in situations where several offspring are synchronously developing as in a clutch of birds, they compete severely for maternal resources often leading to siblicide. In raptors, such competition is manifested in an extreme form, where the elder invariably kills the younger chick reducing the brood size; this might cost to the fitness of the mother (Stinson, 1979) resulting in POC over resources and brood size.

We have suggested that fruits (see cover plate) in plants, in which several developing embryos compete for the common pool of maternal resource, constitute a potential scenario for sibling rivalry and POC (Ganeshaiah and Uma Shaanker, 1988; Uma Shaanker et al., 1988; Bawa et al., 1989). We have investigated these in more detail.

3.1.1 *Can Seeds Distinguish Their Sibs From Non-sibs*

In fruits with several seeds developing simultaneously, each seed can be expected to draw resources more than the mother is selected to offer. In extreme situations this might result in intense sibling rivalry leading to abortion of the weaker seeds (fratricide). However, the intensity with which such fratricide is exhibited would depend on the genetic relatedness among seeds. Consider a pod in which a given developing seed is sharing the limited maternal resources with its genetically related sibs. The seed would loose its inclusive fitness if it indulges in aborting its own sibs. Therefore selection would not favour fratricide under these conditions. On the other hand, if the developing seed is sharing resources with genetically less related sibs it pays for the seed to be very aggressive and to demand additional resources to itself even if it leads to abortion of other seeds (Uma Shaanker et.al., 1988). In other words, fratricide would be expected only if the developing seeds in a pod are genetically heterogenous and not when they are genetically homogenous and similar.

This implies that the seeds developing in a fruit are capable of distinguishing the sibs from non-sibs. We have investigated the existence of such process in plants. Flowers of known cowpea genotypes were crossed with pure and mixed pollen grains from different donors with distinct gene markers and the weight of each seed in a pod was recorded and their parentage was identified using the gene markers in the seedlings (Radha, 1990).

Table 1 provides the seed weights of three genotypes developing with sibs and non-sibs. Clearly, their weights vary depending upon the genetic composition of other seeds in the pod indicating that the seeds are capable of distinguishing the sibs from non-sibs. However the mechanism, through which they do so is still unclear.

Table 1
Average seed weight (mg) of hybrids of donors in pure (sibs) and mixed (non-sibs) cross

Female parent	Cross	Male Parents		
		TVX 118-09E	**APC 1153**	**APC 773**
Virginia	Single	89.76	113.44	96.52
	Mixed	96.96	91.96	96.64
APC 1078	Single	97.56	112.12	121.24
	Mixed	124.36	123.24	118.60
APC 1016	Single	109.48	137.56	129.68
	Mixed	126.04	128.04	114.20
APC 1034	Single	148.04	129.52	127.36
	Mixed	138.28	148.56	139.44

ANOVA, Female parents, P <0.01, Male Parents, P < 0.01

3.1.2 *Seed Abortion In Plants : Fratricide Or Infanticide*

Sibling aggression (fratricide) and hence POC would be more intense in multiovulated species where pod is the unit of dispersal through wind, water or animals (Ganeshaiah and Uma Shaanker, 1988; Uma Shaanker et. al. 1988). In these species by resorting to fratricide, the surviving offspring gains additional dispersal advantage because of the reduced seediness of the fruits (see section 3.3). This is substantiated, by the fact that a large number of species dispersed by wind and water, with pod as unit of dispersal, produce more ovules than mature in to seeds (Table 2) and have a positively skewed distribution of seeds per pod (Ganeshaiah and Uma Shaanker, 1988; Uma Shaanker et al., 1988).

Table 2
Seed to ovule ratio in some wind, water and animal dispersed species

Family and Species	Seed to ovule ratio	Dispersal models
Fabaceae		
Dalbergia sissoo	0.33	Wind
D. oliverii	0.36	"
D. latifolia	0.50	"
D. paniculata	0.40	"
Tipuana tippu	0.21	"
Butea frondosa	0.15	"
Platypodium elegans	0.25	"
Lonchocarpus pentaphyllus	0.30	"
Pterocarpus indicus	0.50	"
Fagaceae		
Quercus gambelli	0.17	Animal
Caesalpinaceae		
Peltophorum ferruginea	0.55	Wind
Tamarindus indicus	0.49	Animal
Combretaceae		
Terminalia arjuna	0.50	Wind/ water
T. tomentosa	0.33	"
Ebenaceae		
Diospyrus montana	*0.45*	*Animal*
Aracaceae		
Cocos nucifera	0.33	Water
Boraginaceae		
Crypthanta flava	0.30	Wind
Lamiaceae		
Salazaria mexicana	0.36	Wind
Sterculiaceae		
Kleinhovia hospita	0.07	Wind/ Water

(from Ganeshaiah and Uma Shaanker, 1988)

Increased dispersal advantage of few seeded fruits is also accrued to the maternal parent through the seeds surviving in such fruits. If this gain, more than compensates for the loss due to seed abortion, maternal parent also may favour the seed abortion. Therefore, it is likely that seed abortion could in fact be a maternal strategy (infanticide) than a consequence of sibling rivalry (fratricide). We tested these alternatives in *Dalbergia sissoo*, a wind dispersed tree species and showed that the abortion in this species is analogous to the Biblical Abel and Cain conflict (Ganeshiah and Uma Shaanker 1988; Uma Shaanker et. al, 1988; Stinson, 1979).

A. *Abel and Cainism in* Dalbergia sisso

In *Dalbergia sissoo*, usually only one of the four or five ovules develops to maturity. The ovules at the stigmatic end that are first to fertilize, dominate and develop more frequently (Fig 1; Ganeshaiah and Uma Shaanker 1988). When the dominant embryos at the stigmatic end are surgically removed, the late fertilized subordinates at the base develop normally indicating that the dominant embryos suppress the development of the subordinates (Fig 2). The process of abortion of the subordinates *perse* is mediated by a killing agent produced by the dominant embryo. This is evident from the increased rate of abortion of subordinate embryos caused by

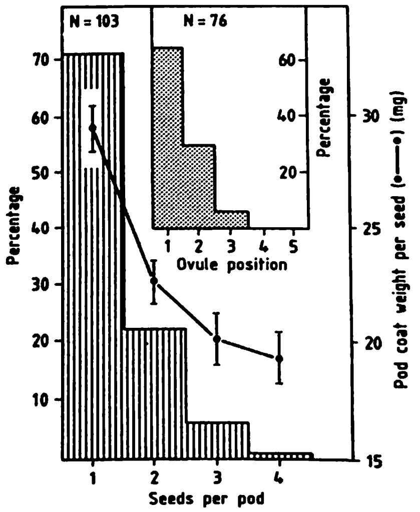

Fig.1 : Frequency distribution of seeds per pod (hatched histogram) and cost of packing (pod coat weight) per seed (line). Inset: Frequency of ovules developing at different positions from the stigmatic end.

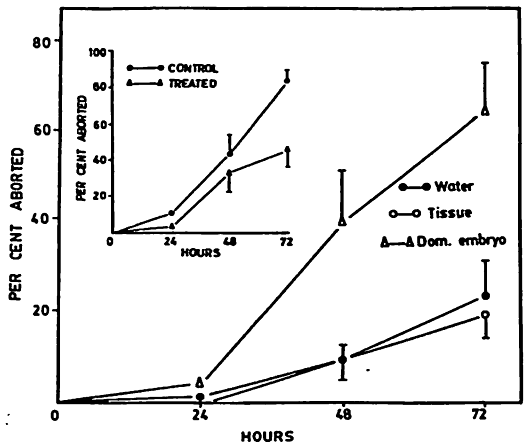

Fig.2 Embryo abortion in *Dalbergia sissoo*. Per cent abortion of subordinate embryos in water, extracts of dominant embryos and of pod coat tissue. Inset: Abortion of subordinate embryos in control pods compared to those in which the dominant embryo is excised (treated).

the water extracts of dominant embryos but not by that of pod tissue (Fig 2). Abortion of seeds in plants thus seems to be due to sibling rivalry (fratricide) than due to infanticide.

B. *Vaginal sealing in* Kleinhovia hospita

In plants the genetic heterogenity among the developing embryos in a pod, originates to a greater part from the genetic differences among the pollen grains. Therefore the sibling aggression among the embryos can also be viewed as a paternal strategy of increasing its own fitness. In accordance with this argument, sibling rivalry occurs in some species at the pre-fertilization stage. We have reported one such mechanism in *Kleinhovia hospita*, a species with wind and water dispersed fruits (Uma Shaanker and Ganeshaiah 1989).

In *Kleinhovia hospita*, as in other wind and water dispersed species, the dispersal efficiency of fruits can be expected to decrease with seed number. This might lead to fratricide among the members of the fruit since the survivor gains additional pod coat to seed weight ratio and hence dispersal advantage. Indeed, out of 15-20 ovules in a ovary, predominantly one develops to maturity (Fig 3; Uma Shaanker and Ganeshaiah 1989). The reduced seed to ovule ratio appears to result from the staggered pollen tube growth by increased concentration of Indole Acetic Acid (IAA) produced by the early fertilised ovules. This eventually inhibits the germination and tube growth of pollen grains ([redacted]) resulting in the prevention of fertilization of rest of the ovules (Fig 3). In other words, fertilization of an ovule by the first arriving pollen grain 'plugs' the style for those arriving later. This effect is similar to the process of vaginal sealing in fishes and insects (Shute, 1958; Parker, 1970), where male that first mates a female, plugs her vagina and thus excludes other males from mating. In this sense, stylar plugging in *Kleinhovia* can also be interpreted as a process of intrasexual selection (see section 3.2).

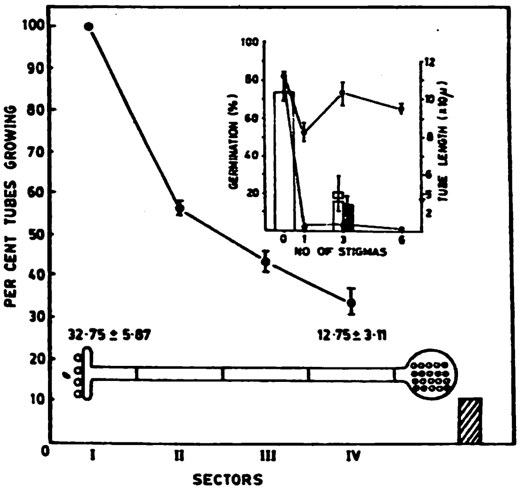

Fig.3: Vaginal sealing in *Kleinhovia hopita*. Percentage of pollen grains growing along different sectors of the style (solid line) and percentage of ovules fertilized (histogram). The number above the stigma indicates pollen grains per stigma in persistent flowers. Inset: Germination percentage (solid line) and tube growth (histogram) of pollen grains in media supplemented with extracts of various number of stigmas from fertilized (close circle; shaded bar) and unfertilized (open circle and bar) flowers.

C. *Offspring can cheat the mother*

If sibling rivalry causes loss in the fitness of the mother, the latter can be expected to develop strategies that prevent such losses. Plants have developed such mechanisms. Selective elimination of few seeded fruits that are formed because of intense sibling rivalry could be one such strategy. Such selective elimination occurs at early stages of the fruit development so that the plant does not expend extra energy on the development of such fruits. Consequently, the aggressive surviving sib in such aborted fruits would be eliminated resulting in a complete loss of its fitness. Interestingly in some species such as *Caesalpinia pulcherrima*, the offspring postpone the abortion (fratricide) to very late stages of fruit development such that the mother would not be able to eliminate them (Uma Shaanker and Ganeshaiah, 1988). Thus in effect the offspring cheat the mother. Consequent to such late intra-fruit abortion of seeds, *Caesalpinia pulcherrima* also bears fruits with few seeds in addition to those with many seeds (Fig. 4).

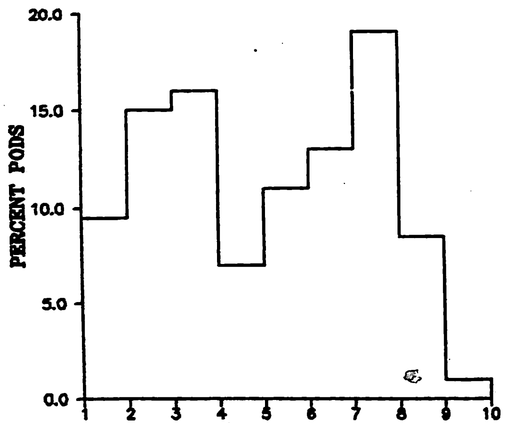

Fig.4 Bimodal frequency distribuion of seeds per pod in *Caesalinia pulcherrima*.

D. *Polyembryony as mother's counter strategy*

Polyembryony, a condition where an additional embryo (mostly from nucellar tissue) is formed along with the zygotic embryo, is a feature unique to angiosperm reproduction. The phenomenon is very wide spread among angiosperms and has been recorded in 244 species from 140 genera belonging to 59 families (Ganeshaiah, et al., 1991). Production of these additional embryos has different consequences to the fitness of the mother and offspring. We have developed genetic and inclusive fitness models to derive the conditions that permit the evolution of polyembryony. It is seen that polyembryony would evolve more easily under the maternal control than that under offspring or selfish endosperm (Fig.5 and 6; Ganeshaiah et al., 1991). In other words, offspring and mother conflict over the production of additional nucellar embryos, the latter always favouring it often against the interest of the former. Therefore, we argue that polyembryony is a maternal strategy to compensate for the loss in her fitness due to seed abortion (brood reduction) caused by the sibling rivalry. This is supported by two empirical evidences: (1) In Citrus, polyembryony was found to be high in species with high brood reduction, (2) Species exhibiting polyembryony are more often those (e.g. species where fruits are dispersed through wind, water, or animals) that frequently exhibit brood reduction (Table 3).

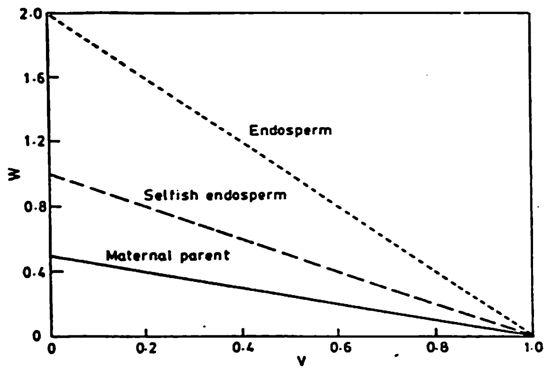

Fig.6 Regions in the parameter space of W, the fitness of the nucellar embryo and V, the fitness of the corresponding zygotic embryo, which permit the spread of the polyembyonic allele. The fitness of the nonpolyembryonic allele is assumed to be unity. Polyembryony can evolve (i) under maternal regulation, in the region above the continuous line, (ii) under selfish endosperm regulation, above the dashed line and (iii) under endosperm regulation, in the region above the dotted line.

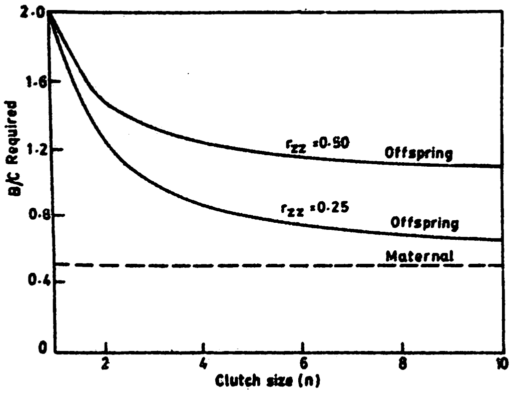

Fig.5 The benefit to cost ratio required for polyembryony to evolve under offspring regulation (solid lines) as a function of clutch size, for two different values of r_{zz}, the coefficient of genetic relatedness between siblings. For comparison, the required ratio corresponding to maternal regulation is also shown in figure (dashed line).

Table 3

Association between polyembryony and the various dispersal modes

		Dispersal mode	
Frequency	Wind	Animal	Explosive
Observed	49	77	44
	(28.8)	(45.3)	(25.9)
Expected	59	30	81
	(34.7)	(17.6)	(47.6)

Chi-square = 92.2; P < 0.001 ; N = 170 species

Expected frequencies were obtained from Uma Shaanker et al., 1990. Values in parentheses refer to percentages.

(from Ganeshaiah et al., 1991).

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3.2 SEXUAL SELECTION IN PLANTS

Why do peacocks have brightly coloured feathers than pea hens, male ungulates have antlers, and some male birds sing differently from females? These features do not contribute to the survival of the species because females of the respective species without them survive as well as males do; rather such traits are costly and might even increase the vulnerability of the males to predation. Darwin (1859) realised that his theory of natural selection does not explain the evolution of such sexually dimorphic traits. He proposed the theory of sexual selection wherein he suggested that such traits have evolved to enhance the reproductive success of the possessor by increasing the probability of gaining access to females. As he postulated, sexual selection has two components : **(a) Female choice,** where females choose the best fit among the competing males based on their secondary sexual traits and **(b) Male competition,** where each male exhibits the secondary sexual traits as elaborately as possible in order to gain dominance over others. In such a war among the males, those with most elaborate secondary sexual characters would be selected.

In the last decade, the concept of sexual selection has been extended to plants to explain the evolution of several reproductive features such as pollen grain to ovule (P/O) ratios (Ganeshaiah and Uma Shaanker, 1982; Uma Shaanker and Ganeshaiah, 1980, 1982, 1984a, 1984b: Willson, 1979), floral sex ratios (Ganeshaiah and Uma Shaanker, 1991; Uma Shaanker and Ganeshaiah, 1984a, 1984b; Vasudeva et al., 1987; Willson, 1979), specialised pollination modes such as polyads and pollinia (Willson, 1979) sexual systems of plants and other floral features (Bawa and Beach, 1981).

3.2.1. *Male Competition in Plants*

In plants, competition among males (pollen grains) for females (ovules) occurs when the number of pollen grains on the stigma exceeds the number of ovules. The intensity of such competition is indicated by the ratio of number of pollen grains on the stigma to that of ovules in the ovary. Analyzing these ratios for 37 species, we found that male competition is a common feature in plants and is more intense in few than many ovulated species (Uma Shaanker and Ganeshaiah, 1990).

In plants, male competition might occur at several stages. For instance, the stigmatic surface of a plant might be swamped entirely by the pollen grains of a competitive genotype pre-empting others from fertilizing the ovules. It is suggested that evolution of pollen transfer units such as polyads, pollinia and viscin threads that hold the pollen grains together could be consequence of such competition during pollination (Ganeshaiah et al., 1986; Ganeshaiah and Uma Shaanker, 1988; Uma Shaanker and Ganeshaiah, 1990).

Male competition might occur in the stylar tissue also where pollen tubes compete to gain access to ovules. An extreme form of such competition is seen in the styles of *Klenhovia hospita.* In this species, pollen grains that germinate early, modify the stigma such that the germination and tube growth of late arriving pollen grains is inhibited (Uma Shaanker and Ganeshaiah, 1989; see section 3.1). Often male competition would extend to the zygotic stage also, where embryos sired by genetically different pollen parents compete severely for resources and resort to killing each other (see section 3.1).

A. *Evolution of pollen grain to ovule (p/o) ratios and floral sex ratios*

Charnov (1979) and Willson (1979) argued that resource allocation to sexes (male and female gametes) in plants would be proportional to the relative reproductive gains accrued through the male (pollen grains) and the female gametes (ovule or seed set). In outcrossed species, a genotype can genetically swamp the entire population through pollen grains. Further, producing pollen grains is less costly compared to ovules (and seeds). Therefore in these species selection can be expected to favour biased resource allocation to males than to females resulting in high pollen grain to ovule (P/O) and male to female flower ratios. We have tested this prediction in a few species.

In *Acalypha fruiticosa,* a monoecious shrub, using artificial dyes, we found that, the probability of pollen flow increases with the height of the plant and the altitude at which they occur (Vasudeva et al., 1987). In accordance with the theory of sexual selection we found that in this species, male to female flower ratio increased with height and altitude of the plant. In *Croton bonplandianum*, the probability of the ovule maturing to seed increases while that of a pollen grain reaching the foreign stigma decreases with age. Sexual selection theory predicts that allocation to males should decrease with age. Indeed we (Uma Shaanker and Ganeshaiah, 1984a) found that the male to female flower ratio decreased with age in *Croton* (Fig.1).

The process of domestication is known to reduce the extent of outcrossing. In accordance with the predictions of the theory of sexual selection, we found that P/O ratios of a set of domesticated species was less than those of their wild relatives. (Table 1; Ganeshaiah and Uma Shaanker, 1982; Uma Shaanker and Ganeshaiah, 1980, 1982).

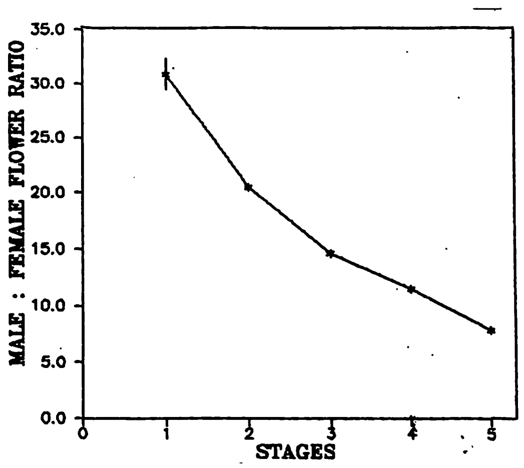

Fig.1 Male to Female flower ratio at five stages of growth in *Croton bonplandianum*. Increase in stages correspond to increasing age classes.

B. *Why are Trees more male biased compared to herbs?*

Trees and shrubs are generally outbreeders compared to herbs. Their prolonged periods of flowering and high investments on elaborate display features to attract pollinators facilitate the effective dispersal of pollen grains. On the other hand, herbs are generally limited in both space and time leading to intense inbreeding within colonies. In other words, in herbs, relatively, a severe local mate competition (Hamilton, 1967) is generated among the pollen grains leading to a reduced average fitness of each pollen grain. Under these conditions selection would favour a biased allocation of resources to males in trees and shrubs compared to herbs. We tested this prediction by estimating the floral sex ratio of 53 monoecious species derived from five families (Ganeshaiah and Uma Shaanker, 1991). Conforming to our prediction, trees were found to be significantly male biased in their floral sex ratio compared to herbs (Fig.2; Ganeshaiah and Uma Shaanker, 1991).

3.2.2. *Female Choice In Plants*

Female choice in plants can be active and or passive. For instance, female can choose by selectively promoting (or preventing) the germination and tube growth of pollen grains or by selectively aborting the embryos (active choice). Alternatively, a female parent can passively choose the best genotype by inciting competition among pollen grains such that the best succeeds. This can be attained by employing strategies that initiate germination of all the pollen grains on a stigma at

Table 1 : Pollen grain to ovule ratio for a few domesticated and wild species

Genus	Domesticated Species / variety	P/O ratio	Wild Species / variety	P/O ratio
Macrotyloma	*uniflorus*	175.08	*uniflorus*	233.33
			accilare	354.28
Vigna	*sinensis*	466.5	*sesquipaedalis*	454.55
			repens	1189.77
Phaseolus	*radiata*	505.00	*atropurpureus*	2251.00
	mungo	505.00	*trilobus*	3764.50
	vulgaris	894.33	*panduratus*	1340.00
	calcaratus	981.00		
Glycine	*max var*	750.00	*max var*	1256.67
	Jupitore		Black Kulti	
Cajanus	*cajan* (annual)	3329.10	*cajan* (perennial)	7134.00
Eleusine	*coracana*	1534.00	*africana*	2978.00

Analysis between domesticated and wild species within a genus carried out ; $P < 0.01$ Uma Shaanker and Ganeshaiah, 1982.

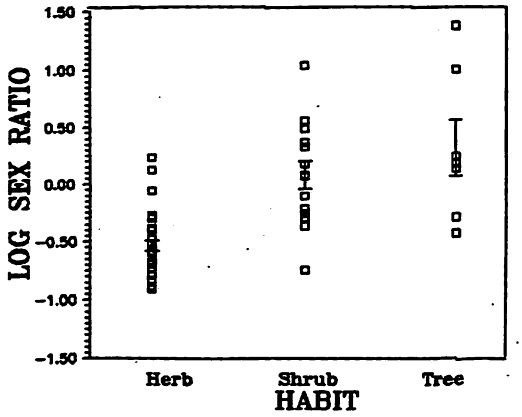

Fig.2. Log male to female flower ratios of herbs, shrubs and trees of 53 monoecious species. The vertical bars indicate standard error of mean.

once. We have found that plants employ two such strategies.

A. *Incitation of male competition through pollen grain reception strategies*

In some plants, pollen grains are deposited instantaneously in large loads on the stigma such that all the pollen grains enter the competition to fertilize the ovule at once. In these species flowers once pollinated would receive pollen grains more than the ovule number (Uma Shaanker and Ganeshaiah, 1990). However, depending upon the frequency of flowers that get pollinated and the mode of pollination, often a small percentage of flowers receive pollen grains less than the ovule number. Accordingly three different kinds of distribution patterns of pollen grains on stigma are observed (Uma Shaanker and Ganeshaiah, 1990).

a) Negatively skewed distribution :

In some species, most of the flowers receive pollen loads greater than the mean ovule number per ovary ensuring that there is a potential for competition among the pollen grains to fertilize the ovules.

b) Discontinuous bimodal distribution :

In few species that are pollinated by large insects, flowers contain either a very large load of pollen grains on the stigma if they are visited by the pollinator or none at all if they are not. This results in a bimodal distribution of pollen grains per stigma.

c) Continuous bimodal distribution :

This distribution is essentially similar to that of discontinuous bimodal except that a small frequency of flowers obtain intermediate loads of pollen grains as a result of accidental pollination.

All these mechanisms generate instantaneous and large loads of pollen grains on the stigma and promote the en masse germination of pollen grains at an instant of time resulting in a severe male gametophytic competition among the germinated pollen grains to fertilize the ovules.

B. *Stigmatic regulation of pollen grain germination*

In some species, where pollen grains accumulate gradually, incitation of male competition is generated by restricting their germination till a certain number (greater than the ovule number) is deposited on the stigma. We have reported one such mechanism of female incitation of male competition *in Leucaena leucocephala* (Ganeshaiah and Uma Shaanker, 1988).

Stigma of *Leucaena leucocephala* has a pouch containing a viscous fluid at pH 5.0 into which pollen grains are deposited. Pollen grains less than a critical number (<25; less than the mean ovule number per ovary) in the pouch do not germinate. We found that this is regulated by a proteinaceous inhibitor of pollen grain germination which is active at stigmatic fluid pH of 5.0. However, pollen grain numbers greater than this (>25) can additively raise the stigmatic fluid pH to 6.0. This change in pH inactivates the inhibitor and thus allows all the pollen grains to germinate at once (Fig.3). In effect, this

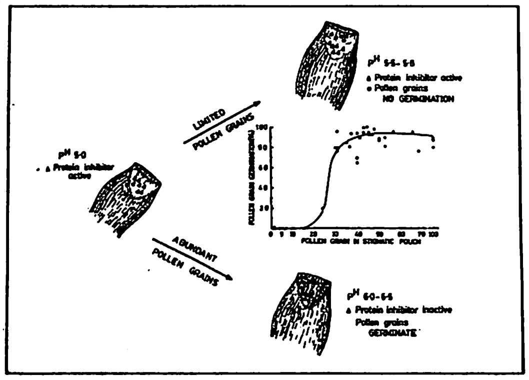

Fig.3 Stigmatic inhibition of pollen grain germination in *Leucaena leucocephala*. The stimatic fluitd with pH 5.0 has a protein inhibitor of pollen grain germination. Limited number of pollen grains in the stigmatic pouch (<25-30) do not germinate since raise in pH is only marginal and the inhibitor is active. Abundant pollen grains germinate because they raise the pH to 6.5 and thus inactive the inhibitor.

Inset : Relation between pollen grain number in the stigmatic pouch and their germination percentage *in vivo.*

mechanism ensures an intense competition among the pollen grains such that the best among them fertilise the ovules.

Such number dependent inhibition of pollen grains by the stigma has also been reported in a few other species such as *Moringa* (Uma Shaanker and Ganeshaiah, 1990).

C. *Genetic basis of male competition and female choice*

An important assumption of the theory of sexual selection (in plants) is that the differences among the pollen grains in their competitive ability to sire ovules is genetically based and that stigmas are capable of differentiating these genetic differences among the pollen grains (female choice). Unfortunately little is known about this.

An elaborate crossing programme was taken up in cowpea to study the genetic basis of male competition and female choice (Radha, 1990). The study involved three pollen donors with distinct gene markers and four female parents. Male competition at the stigma was simulated by applying a mixture of pollen grains from all the three donors on each female. It was found that pollen donors differed significantly in their probability of siring seeds and these differences were consistent within each female. Further, the competitive ability of the donor was correlated with the germination and tube growth of their pollen grains. However, pollen donors that were successful in siring significantly higher number of seeds over a female parent were not necessarily so over another female parent. These results indicate that while males differ genetically in siring ovules, females exercise choice over the male donors. But the precise mechanisms involved in this process is not yet known.

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3.3 DISPERSAL MODE AS A SELECTIVE FORCE

Plants disperse their reproductive propagules, seeds and fruits through abiotic (wind and water) and biotic (animal) agents. The efficiency of dispersal by these modes depends considerably on several features of fruits and seeds. For instance the dispersal efficiency of fruits is related inversely to their wing loading (ratio of weight to surface area) in species dispersed by wind and water (Ganeshaiah and Uma Shaanker, 1988; Uma Shaanker et al., 1988; Ganeshaiah and Uma Shaanker, 1991) and directly with their pulp to seed weight ratio in animal dispersed species (Uma Shaanker et al., 1988; Hegde et al. 1991 a, 1991b). Dispersal efficiency in these species can be enhanced by decreasing the individual seed weight and/or seed number per furit (clutch size). In otherwords, selection for enhanced dispersal efficiency in species with fruit as a unit of dispersal favours reduced seed size and/or a small clutch size. In contrast, in species where seeds are dispersed passively, their dispersal efficiency is independent of their weight; in them, the clutch size and individual seed size will be shaped by other selective pressures such as the cost of packing the seeds in fruits (Ganeshaiah et al., 1986; Uma Shaanker et al., 1988) and seedling establishment (Smith and Fretwell, 1974; Uma Shaanker et al., 1988) respectively. Thus depending upon the unit and the mode of dispersal adopted by a species, selection to enhance dispersal efficiency would shape several seed and fruit features in plants.

3.3.1. *Dispersal Mode and Clutch Size*

In species where the entire fruit is dispersed as a unit, few seeded pods have a better dispersal advantage than those with many seeds because of their better wing loading (weight to surface area ratio). For example, in *Dalbergia sissoo,* a wind dispersed tree, we (Ganeshaiah and Uma Shaanker, 1988) found that single seeded pods have a better wing loading compared to two and three seeded pods. Consequently single seeded pods are dispersed to farther distances than those with two and three seeds. In such species, selection to enhance the dispersal efficiency can be expected to favour pods with few seeds. Indeed the frequency distribution of seeds per pod in *Dalbergia sissoo* is highly positively skewed with nearly 70 to 80 percent of them having only one seed (Fig.1).

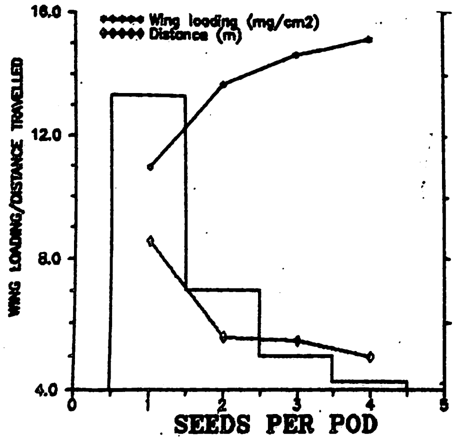

Fig.1 Wing loading (weight:surface area) horizontal dispersal distance and frequency distribution (histogram) of pods with varying number of seeds in *Dalbergia sissoo.*

On the otherhand, in passively dispersed species, where the dispersal efficiency is not related to seediness of fruits, cost of packing seeds is the major factor influencing clutch size. Since the fixed cost of packing (such as peduncle and flower weight) is shared by all seeds in a fruit, packing cost per seed can be minimized by loading many seeds. Thus in these species, selection favours a negatively skewed distribution of seeds per fruit.

In *Leucaena leucocephala,* a passively dispersed species, we found that the distribution of seed number per pod is negatively skewed with pods containing many seeds (Ganeshaiah et al., 1986). The mode of the observed frequency distribution of seeds per pod corresponded to that for which the cost of packing each seed was least (Fig.2); in otherwords, selection for minimizing the cost of packing seems to have shaped the clutch size in *Leucaena leucocephala.*

Occasionally however, the frequency distribution of seed number per fruit would be shaped by both, dispersal efficiency and cost of packing seeds in pod. For example, in *Albizzia* and *Acacia,* the flat pods are carried away by the wind though occasionally they disperse the seeds passively. Therefore one would expect that in these species, the frequency distribution of seed number would be shaped by both dispersal efficiency (favouring small clutch size) and packing cost (favouring large clutch size). Indeed in *Albizzia* and *Acacia,*, the seed number per pod is normally distributed (Uma Shaanker et al., 1988), indicating perhaps the role of the above two selective forces in shaping seed number per fruit.

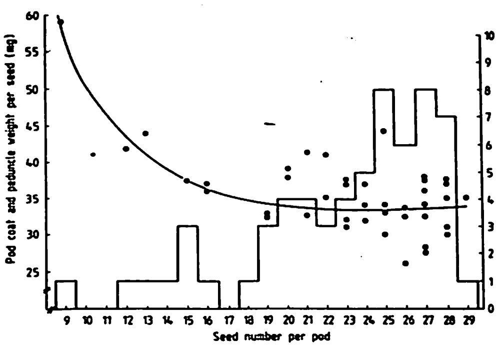

Fig.2 Cost of packing (pod coat and peduncle weight) per seed (solid line) and frequency distribution (histogram) of seed number per pod in *Leucaena leucocephala*.

3.3.2. *Dispersal Unit and Clutch Size*

In addition to dispersal mode, the unit of dispersal also plays an important role in shaping the clutch size. In fact dispersal mode shapes the clutch size only if the whole fruit is the unit of dispersal. In species where seeds are dispersed through wind, water, animals or passively, packing cost is the major selective force in shaping clutch size. Accordingly, species with fruit as the unit of dispersal can be expected to have smaller clutch size compared to those with seed as the unit of dispersal.

Analyzing the dispersal unit and the frequency distributions of seeds per fruit of 75 species, we (Uma Shaanker et al., 1988) found that species with fruit as a dispersal unit had more frequently positively skewed distribution of seed number per fruit, while those with seed as dispersal unit had more frequently negatively skewed distribution.

Further, comparing the clutch sizes and dispersal units of 855 species we (Uma Shaanker et al., 1990) found that species in which the fruits are dispersed through wind or animals have a smaller clutch size (less than 4) than those in which seeds are dispersed passively (Table 1).

A. *Fruit preference criteria of avian frugivores and clutch size*

In animal dispersed species clutch size may also be shaped by the preference criterion adopted by the dispersers while foraging. For instance, preference based on pulp to seed weight ratio would favour a small clutch size while that based on the total pulp reward a large clutch size. If the preference is based on ratio of benefit (energy reward) to the cost (energy spent) of handling the fruits, selection would favour the clutch size that provides the dispersers the maximum ratio of benefit to cost (Hegde et al., 1991a).

Solanum pubescens, produces red spherical berries foraged by Red vented Bulbuls (Hegde et al., 1991a). When bulbuls were offered fruits of different sizes, they preferred medium sized fruits significantly more frequently than small or large fruits (Fig.3a). The preferred size class of fruits were found to offer the birds the maximum ratio of benefit (pulp weight) to the cost (time spent in handling the fruit). The seed number per fruit in *Solanum* was normally distributed with the mode corresponding to the size class of fruits preferred by the bulbuls (Fig.3a)indicating that the preference criterion adopted by birds plays an important role in shaping the clutch size.

Table 1

Distribution of species into classes of dispersal mode and clutch size

Dispersal mode		Ovule number per ovary 1-4	5-10	10
Wind	Obs.	243	15	55
	Exp.	147	25	141
Animal	Obs.	68	15	59
	Exp.	71	12	68
Passive	Obs.	90	39	271
	Exp.	188	32	180

Chi-square = 219.83 ; P < 0.001 ; df = 4 ; N = 855 species

Expected values were derived assuming a random distribution. (from Uma Shaanker et al., 1990)

3.3.3. *Dispersal Mode and Seed Size*

Assuming that the seedling fitness (vigour) increases at a decreasing rate with seed biomass (size), Smith and Fretwell (1974) argued that the maternal parent would be selected to allocate an optimal amount of resource (m*) into each seed such that the ratio of seedling fitness to the seed mass is maximisied. However, such prediction might not

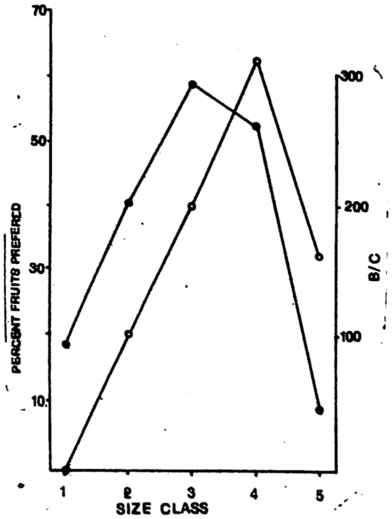

Fig.3a Percent perference (open circles)and benefit to cost ratio (B/C; closed circles) of fruits of various size classes in *Solanum pubescens*.

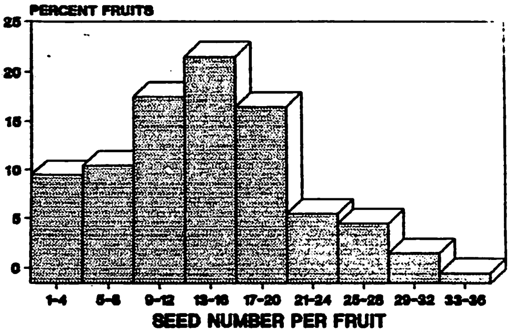

Fig.3b Frequency distribution of seed number per fruit in Solanum pubescens. The mode of the distribution corresponds to the size class of fruits preferred by t he birds (see fig.3a).

often be true because, in addition to seedling fitness, the offspring fitness may also depend on other components of fitness such as dispersal efficiency of fruits. For instance, in species where the fruit is dispersed as a unit, the dispersal efficiency decreases with increase in seediness. In such species, with single seeded fruits, seed size would be selected as a trade off between the two selective forces, namely seedling establishment favouring increased seed size and dispersal efficiency favouring a reduced seed size.

A. *Seed size as a trade-off between seedling establishment and fruit dispersal efficiency*

a. *Butea monosperma*

Butea monosperma produces single seeded indehiscent pods dispersed by wind and /or water (Ganeshaiah and Uma Shaanker, 1991). In this species dispersal efficiency as indicated by the wingloading of pods decreased with seed size while seedling fitness measured as leaf area increased with seed size (fig.4). Thus in *Butea*,dispersal efficiency favours small seeds while seedling fitness favours large seeds. The seed weight in *Butea* was normally distributed and its mean (and mode) was more than that predicted by dispersal efficiency and less than that predicted by seedling establishment (Fig.4).

b. *Santalum album*

Santalum album, an endemic tree of South India, produces single seeded spherical berries (Hegde et al., 1991b). Koel, being the predominant disperser of *Santalum*, swallows the entire fruit and regurgitates the large seeds under and around the canopy or defecates small seeds far away from the tree. In otherwords, the defecated seeds are carried far away from the parent tree and thus gain dispersal advantage compared to the regurgitated seeds. Thus selection for dispersal efficiency favours smaller seeds. On the otherhand, selection for seedling establishment favours large seeds because seedling leaf area was found to increase monotonically with seed size. The observed seed size distribution in *Santalum* corresponds to that expected as a trade-off between the above two opposing selective pressures on seed size.

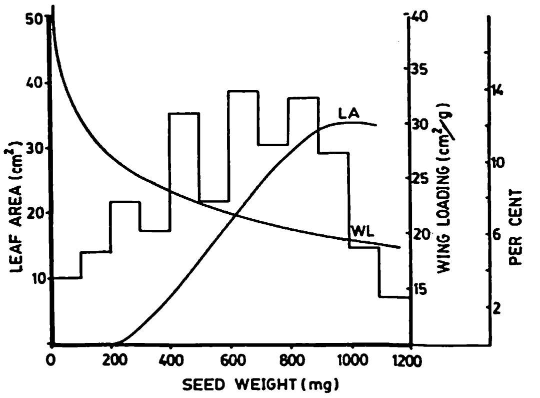

Fig.4 Relationship of wing loading (surface area weight:WL) and seedling fitness (leaf area;LA) with seed weight in *Butea monosperma*. The frequency distribution of seed weights is superimposed (histogram).

3.3.4. *Dispersal Mode and Seed Chemical Composition*

Dispersal efficiency in wind, water and animal dispersed species can be enhanced by reducing the seed weight. This can be attained by packing energy in the form of fat or protein than carbohydrate, because such process reduces seed weight without altering the energy content. Therefore in species where the dispersal efficiency decreases with the seed mass (in wind, water and animal dispersed species), selection should favour packing proportionately more fat than carbohydrates. On the otherhand, in species where the dispersal efficiency is independent of seed mass (in passively dispersed species), selection favours packing energy in the form of carbohydrate than fat because synthesising fat is relatively costly. Analyzing the seed chemical composition of nearly 770 species, we (Lokesha et al., 1992) found that seeds of wind and animal dispersed species had significantly higher proportion of fat and less of carbohydrates compared to the seeds of those dispersed passively (Fig.5). Further, the wind and animal dispersed species also had a significantly small seed size compared to those dispersed passively. In otherwords dispersal mode plays an important role in shaping the seed chemical composition.

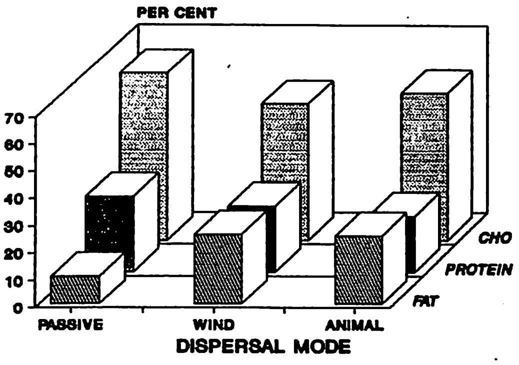

Fig.5 Chemical composition of seeds of species of different dispersal modes (N for species:passive=229; wind=240; animal=301).

3.3.5. *Association Between Dispersal Mode and Pollination Mode*

Dispersal of pollen grains and seeds are the two important means by which plants attain their reproductive success. Both these, require the mediation of vectors such as wind, water, insects or animals. These vectors are common for both and are often limited in a habitat. Therefore selection can be expected to favour adaptation of plants to the same mode (vector) for both pollination and dispersal. Further, use of the same mode for both pollination and dispersal is advantageous because features evolved to facilitate wind pollination might also predispose it for wind dispersal; similarly display features evolved to attract insect or animal pollinators might also be extended to attract animal dispersers. Thus, it could be predicted that species pollinated by wind, are likely to be wind dispersed, and those pollinated by insects and animals, are likely to be dispersed by animals.

Analyzing the dispersal and pollination mode of 812 species from the Flora of British Isles, we (Uma Shaanker et al., 1990) found that more often than expected wind pollinated species have wind as dispersal mode and insect pollinated species have either passive (including explosive) or animal dispersal mode (Table 2). In otherwords, there appears to be a strong association among the modes of pollination and dispersal. We suggest that such associations might be due to simultaneous adaptation of plants to the predominant vector of the habitat by both these life history traits. Alternatively such association could be due to the adaptation of one of the life history traits to the predominant vector of the habitat, the other having been shaped as a pleiotropic consequence.

Table 2
Distribution of species into classes of dispersal and pollination modes

Pollination mode		Dispersal mode Wind	 Animal	 Passive
Wind	Obs.	73	7	14
	Exp.	33	17	45
Self	Obs.	25	10	49
	Exp.	26	13	35
Insect/	Obs.	186	126	322
Animal	Exp.	225	112	304

Chi-square = 91.16; P 0.001; df = 4; N = 812.

Expected values are derived assuming random distribution (from Uma Shaanker et al., 1990).

3.3.6 *Dispersal Mode And Vulnerability of Extinction*

Destruction of natural habitats is proposed as a major reason for species being rendered as Rare, Endangered or Threatened (Lucas and Synge, 1978). However, in recent years, features intrinsic to the plants have also been proposed to lead to the threatened status of the species (Kruckeberg and Rabinowitz, 1985). In an analysis of 487 rare, endangered and threatened (RET) plant species of South India, Lokesha et. al., (1991) found that RET species are more likely to be those that are dispersed by animals and less through wind, water or by passive means (Table 3). This indicates that species dependent on animal dispersal are more prone for being endangered or threatened. The vulnerability of these species for extinction is accentuated further by the fact that there exists a strong association between the dispersal and pollination modes (see previous section). Thus perturbations in the environment that disturb the biotic vectors, affect the dispersal of both the gametes and the seeds, fruits, aggravating the probability of extinction.

Table 3
Distribution of Rare, Endangered and Threatened species into classes of dispersal modes

Dispersal mode	observed	Expected
Animal	186 (38.19)	86 (17.66)
Wind/Water	117 (24.02)	170 (34.91)
Explosive	184 (37.79)	231 (47.43)

Chi-square = 142.0; P< 0.001; df = 2; N = 487

*Computed based on the data from Uma Shaanker et al., (1990) (from Lokesha et al., 1991).

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3.4 FRACTALS, SELF ORGANIZATION AND PLANT REPRODUCTIVE FEATURES

Understanding the physical basis of the patterns in biology is an exciting field. Such treatment has infact been attempted time and again; the monumental work of D'Arcy Thompson (1942) for instance has made a significant influence on our understanding of the shapes and sizes of living systems. Of recent, some of the developments in physics and stochastic mathematics (e.g., the process of self-organisation, fractals and chaos) have helped a great deal in offering simple explanations for the apparently most complicated behavioural features such as social activities in insects, shapes of a few biological structures and dynamics of natural populations. We have found that some of the plant reproductive features can infact be simply understood using some of these concepts.

3.4.1. *What Is Common Between Size Of Words And Size Of Seeds ?*

Angiosperms exhibit a wide range of variation in the size of the individual seeds ranging from few micrograms to as high as few kgs. But which among them are more frequent and why is a question not generally addressed. *Apriori* there is no basis on which any specific pattern could be expected for the frequency distribution of mean seed size in plants. However, analysing seed sizes of 1413 species, we found that the frequency of seed sizes was highly positively skewed with disproportionately more species having smaller size (Fig.1: for wind dispersed species; Hegde et al., 1991). Further such a distinct hollow distribution persisted for any range of seed sizes indicating scale invariance in their distribution pattern — a characteristic feature of fractal distribution (Mandelbrot, 1977).

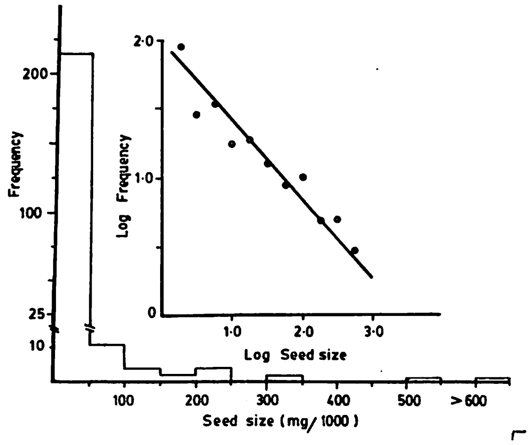

Fig.1. Frequency distribution of seed size in wind dispersed species (N=238). Inset: Log-log plot of frequency and seed size.

Recently it has been shown that the frequency distribution of personal income levels, number of publications by scientists, size of taxa and size of words follow fractal relation (West and Shlesinger, 1990). These distributions are governed by an inverse power law given by $Y \alpha x\,\hat{}a$ where Y = frequency and x = size. We found that the seed size distributions also fitted to this equation indicating their fractal nature (Table 1). The slope (~ -.50; Fig.1) indicated that frequency of species with a given seed size is inversely proportional to the square root of their seed size (Hegde et al., 1991).

Table 1
Regression coefficients for the log-log plot between frequency and seed size and skewness coefficients for various groups.

Groups	N	Slope	R2	Skewness*
Dispersal modes				
1. Wind	238	-0.56	93	7.64
2. Animal	300	-0.41	85	10.39
3. Passive	225	-0.41	78	6.23
4. Total a	815	-0.51	90	15.45
Families				
5. Leguminosae	565	-0.49	55	10.77
6. Compositae	143	-0.58	60	3.43
7. Total b	1413	-0.59	87	24.52

*All the coefficients were significant at $P < 0.001$. (from Hegde et al., 1991).

Smaller seeds can occupy and establish in small habitats while large seeds always require large sites. Hence availability of suitable germination sites might shape the frequency distribution of seed size. It is observed that habitat sizes are also fractally distributed. Therefore we suggest that the observed fractal distribution of seed sizes might be a consequence of the availability of habitats for the seeds.

3.4. 2 Pods As Self Organised Pots

Plants exhibit a few specific patterns of distributions of seeds per fruit (Uma Shaanker et al., 1988). These patterns are amazingly consistent within each species (with respect to their skewness coefficients) and are generally independent of extrinsic features; rather they seem to be highly regulated by factors intrinsic to the system. It is also surprising that these distinct patterns arise from an initial symmetric condition where all the ovules are equally capable of developing. The phenomenon where such initial symmetry breaks down and gives way to an asymmetric pattern can be explained as an autocatalytic feedback of the initial stochastic differences among the elements of the system resulting in a self organised structure (of the system). Several social activities of insects have been explained based on such accumulation of the differences among the members of the colony by an autocatalytic process resulting in distinct behavioural patterns at the colony level (Deneubourg et al., 1989). We have shown that the distinct frequency distributions of the fruits can infact be explained as a process of self organisation (Ganeshaiah and Uma Shaanker, 1992).

Consider a fruit with its ovules as a pot with several sinks competing independently for the limited resources offered in bouts of small units by the mother plant. Also consider the probability that a given ovule gets the next bout of resource (Pi) is a function of its history — how many resource units it has already gathered (Yi) relative to others and is given by the famous Polya equation

$$Pi = \frac{[Yi + k]^{\wedge\ x}}{\sum_{i=1}^{n} [Yi + k]^{\wedge\ x}}$$

where $\dot{x}$ = the power function that defines the sink drawing ability of ovules and is equal for all ovules, and n = number of ovules.

It can be seen that by varying merely x, the sink drawing ability of the ovules it is possible to generate the fruits with varying number of seeds (Fig.2). Interestingly such process could also generate specific distribution patterns of seeds per fruit by merely varying the x values. The natural distribution patterns and those simulated were similar in several features (Fig.3a and 3b; Ganeshaiah and Uma Shaanker, 1992) indicating the possible similarity in the underlying process that generates them. Thus the development of fruits appears to be a consequence of self organised development of individual seeds (elements) of the fruit (system).

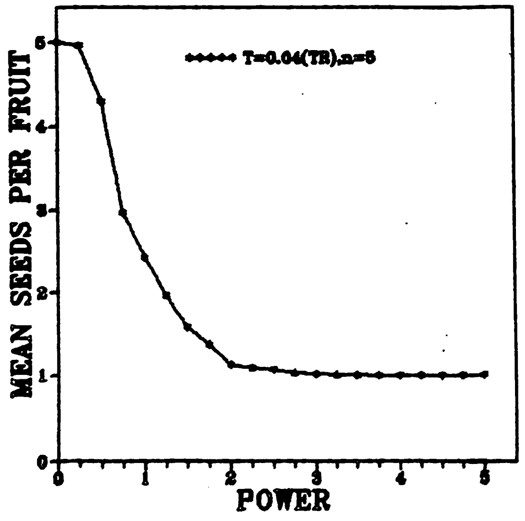

Fig.2 Relationship between the mean seed number per fruit and the power, defining the sink drawing ability of ovules. Simulation was run assuming 5 ovules per ovary (n) and an initial resource status of the ovule, T equal to 4 percent of the final seed weight (TR).

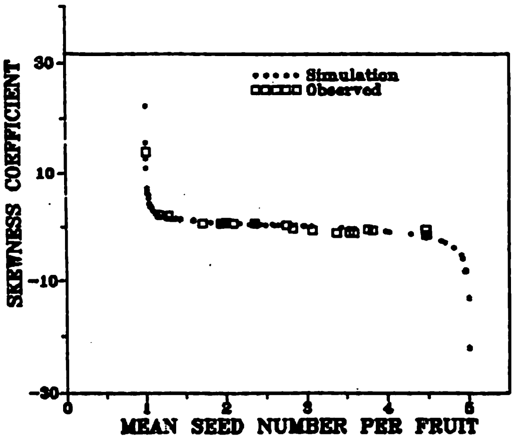

Fig 3a. Relation between the skewness co-efficient of the frequency distribution of seeds per fruit and the main seed numberper fruit obtained from simulation(n=5;T=0.04*TR; for notation see legend of (Fig.2) Open squares represent observed data for 18 species.

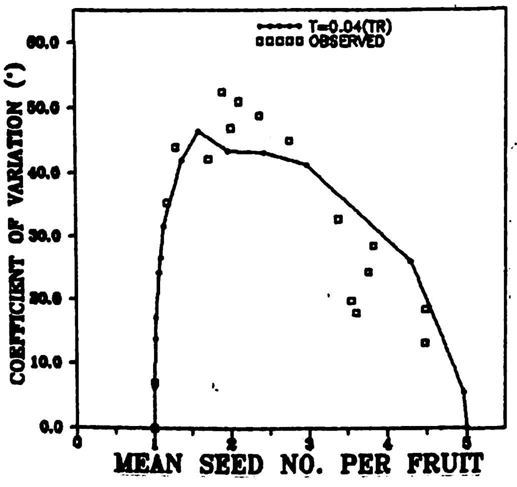

Fig.3b. Relation between co-efficient of variation and the mean seed number per fruit obtained from simulation(n=5;T=0.04*TR; for notation see legend of (Fig.2)open squares represent observed data points per 18 species .

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4. THESES AND PROJECTS

4.1 THESES

4.1.1. *Components of sexual selection in Vigna unguiculat ; (L.) Walp.*

Student : Mrs M.R. Radha
Major Advisor : Dr. K.N. Ganeshaiah

Summary : The investigation was taken up to study the components of sexual selection in plants. Seven cowpea genotypes were involved in an elaborate crossing programme using three male and four female parents. Pollen grains of male genotypes were mixed and used to pollinate the stigmas of the females parents. The results indicated that the male genotypes differed significantly in siring seeds in a pod. The male genotypes also differed with respect to the position at which they sired the seeds in pods, indicating differences in competitive ability for the tube growth along the style. These features however were found to be influenced by the female genotypes also indicating an interaction between male and female genotypes over the fertilization of ovules.

The males differed in their germination percentage and rate of pollen tube growth when studied on their own stigmas *in vitro.* However, the pollen grain germination and tube length of different donors varied on the stigmas of different females, indicating the male—female interactions. The male genotypes which produced the longest pollen tubes over the stigma of a particular maternal parent, infact, sired maximum number of seeds at the basal or middle portion of the rod.

Though males were found to differ in pollen features such as germination and pollen tube growth rate, no significant association was observed between the performance of the genotypes at the gametophytic and sporophytic levels.

4.1.2. *Parent-offspring conflict over seed dormancy in plants*

Student : Mrs M.R. Radha, Ph.D. scholar
Major Advisor : Dr. K.N. Ganeshaiah

Summary : Parent-Offspring Conflict (POC) occurs in several situations in plants such as seed development, seed number per fruit and post—dispersal competition among sibs. Ellner, (1986) proposed that POC can occur over dormancy imposition in seeds. He suggested that maternal parent would be selected to impose dormancy among the offspring in order to reduce post-dispersal competition and the consequent loss in her inclusive fitness. However, being dormant for a longer period would result in increased mortality for the offspring imposed with dormancy compared to those not imposed with. Therefore he suggested that the interest of the offspring might not coincide with that of the mother and hence they might conflict with each other over dormancy. Unfortunately, there are no studies as of yet demonstrating POC over seed dormancy in plants. The investigation is therefore aimed at studying the following objectives:

a. Interaction among the maternal and offspring tissue of seeds in imposing and breaking the dormancy.

b. Testing the fitness of the mother and the offspring with and without dormancy.

c. Dormancy release patterns of seeds developed under varying levels of genetic relatedness among themselves and with the mother.

4.1.3. *Proximate causes of embryo abortion in plants with reference to* Deerris indica *Lam and* Syzigium cuminii *(L.) seels.*

Student : Mrs H.S. Arathi
Major advisor : Dr. K.N. Ganeshaiah

Summary : The study was aimed at identifying the proximate mechanisms involved in embryo abortion in two tree species viz., Pongamia (*Derris indica*) and Syzigium *(Syzigium cuminii)* which exhibited persistent embryo abortion. In Pongamia, predominantly one of the two ovules develops to seed while in Syzigium, invariably only one of the thirty ovules develops to seed.

In both the species, pollen limitation, incompatibility and resource limitation failed to explain embryo abortion. Rather post fertilization abortion of embryos was found to be the major factor responsible for reduced seed to ovule ratio. However the mechanism of embryo abortion differed between the two species.

Syzgium: In this species embryo abortion was preceded by the establishment of a dominance hierarchy among the fertilized ovules. The early fertilised ovules generally became dominant while those fertilised late were weak and eventually aborted. The mechanism of abortion of the subordinate ovules was tested by treating the developing ovules with the extracts of the maternal tissue (fruit wall) and that of the dominant ovules. The results suggested that the abortion is mediated by certain chemicals produced by the dominant embryos but not by the maternal tissue. When the extract of the dominant ovules was treated with silver thiosulphate (STS, known to inhibit the action of ethylene) the rate of embryo abortion retarded. Further spraying the young developing fruits with STS where abortion had not yet set in, resulted in fruits with more than one seed. These results indicated that embryo abortion in Syzigium is brought about by the dominant ovules through an ethylene mediated phenomenon.

Pongamia: In this species the abortion was not mediated by any killing agent. Rather abortion was found to be a consequence of starving the young subordinates by the strong sink activity of the early fertilised dominant ovules. This was evident from the increased 14c activity realised in the subordinate ovules when they were alone in the fruit compared to when they were with the early dominant ovules (Fig.1).

Thus embryo abortion in Syzigium and Pongamia appears to be a manifestation of sibling rivalry but not under the maternal regulation. This indicates that sibling rivalry and the consequent parent-offspring conflict might be a wide spread phenomena in plants.

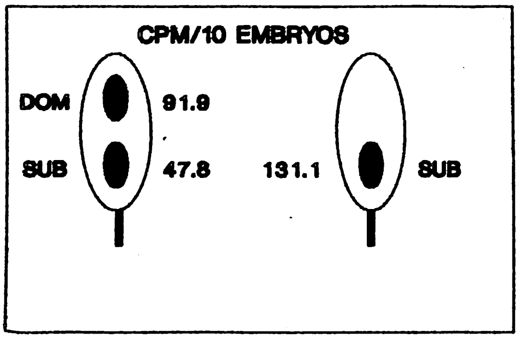

Fig.1 Uptake of ^{14}C-source (25uci) by subordinate embryos in the presence (left) and absence (right) of the dominant embryo in pods of *Derris indica*. Data are average of 150 embryos from the experiments.

4.1.4. *Consequences of inciting mate competition to the female reproductive success in plants.*

Student : Mr.R. Vasudeva, Ph.D. Scholar
Major Advisor : Dr K.N. Ganeshaiah

Summary : In plants, female parents are known to incite intense mate competition by adopting certain strategies that increase the genetic diversity among the pollen grains at the stigmatic level. Though this might benefit the female in terms of harvesting the best pollen grain to fertilise her ovules, it may also results in an increased diversity among developing embryos. The consequent reduction in the genetic relatedness among the developing offspring leads to an intense sibling rivalry over resources. In extreme situations, this results in abortion of weak seeds reducing the brood size and hence cost to the fitness of female parent. In other words indiscriminate incitation of mate competition by female might cost her fitness. This could be called as cost of sexual selection. The present investigation is intended to study such consequences of female incitation of gametophytic competition to her reproductive success in multiovulated species. Studies conducted on two plant species, *Phaseolus latheriodes*, and *Hibiscus canabinis* have shown the following preliminary results.

The mean seed number per fruit in *Phaseolus latheroides* decreased with the increase in number of pollen donors. However, the mean seed weight was higher when pollinated with single or five donors compared to selfed seeds, pollination with twenty donors gave the highest seed weight among all. Whether the ultimate fitness of the plants in various crosses varies would be tested by measuring the seedling fitnesss features.

The cost of sexual selection might also operate at pre-pollination level. Out crossing plants would frequently compete in terms of pollinator attraction and pollen delivery in a variety of ways. Several workers have recorded increased visitation rates of pollinators with the increase in floral display features (e.g. size of inflorescence and flower) and/or floral rewards (e.g. nector). Such selection for increased floral visitation may also influence the visitation of floral predators. This is analogous to the situation in tungara frogs where highly vocal males, called 'chuck males', apart from attracting more number of receptive females, also attract greater number of predatory bats compared to the less vocal males. However, there are no reports in plants showing that strategies to increase the pollinator visitation would also increase predators. In three outcrossed species viz., *Solanum pubescens, Derris indica* and *Cassia fistula* association between visitation rates of pollinators and floral predators was studied. Briefly the results are as follows :

a. In *Solanum pubescens*, the number of flowers displayed per inflorescence was positively correlated to the number of flowers predated.

b. Trees of *Cassia fistula* with higher display ranks were found to be infested more with a specific pyrid larvae that feeds on floral structures.

c. In *Derris indica* a substantial fraction of the flowers are turned into galls by a group of insect parasites costing to the female parent. The fruit set percent in this species was positively correlated with percent flowers that turned into galls implying that the attraction to pollinators had a positive influence on attraction to floral predators.

4.1.5. *Physiological basis of embryo abortion in a wind dispersed tree,* Dalbergia sissoo.

Student : Mr P. Mohan Raju
Major Advisor : Dr R. Uma Shaanker

Summary : The study was aimed at investigating the physiological basis of intra-pod embryo abortion in a wind dispersed tree, *Dalbergia sissoo* in which predominantly, only one of the 4 or 5 ovules develop to maturity. Abortion is found to be a consequence of the establishment of a dominance hierarchy among the developing embryos (Ganeshaiah and Uma Shaanker, 1988).

Two alternative models were investigated: a) chemically mediated abortion of subordinates by the dominant embryo and b) starving the subordinate by the dominant embyo.

The salient findings are as follows :

a. Subordinate embryos in presence of dominant embryos exhibited a very low uptake of labelled sucrose. In contrast, when the dominant embryos were excised from the pods, the subordinate embryos exhibited a specific activity equal to or more than the dominant.

b. The uptake of labelled sucrose by subordinate embryos was inhibited more by the aqueous extracts of the dominant embryos than those of pod coat tissue or of unfertilized ovules (Fig.2).

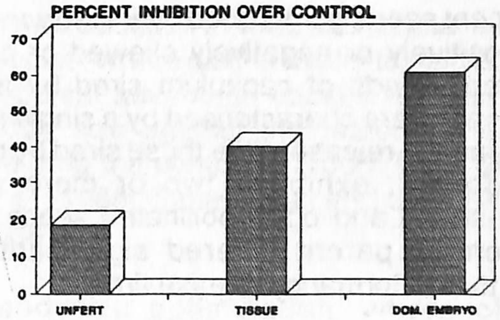

Fig.2 Per cent inhibition over control of ^{14}C sucrose (25uc) uptake by embryos incubated extracts of unfertilized ovules, pod coat tissue and of dominant embryos in *Dalbergia sissoo*

c. Exogenous application of a growth regulator mixture (auxin, gibberlic acid and kinetin) immediately following fertilisation reduced the rate of embryo abortion in the pods.

These results suggest that in *Dalbergia* the dominant embryos produce a chemical that starves the subordinates by suppressing their resource drawing ability. However, the exact mechanism and the nature of the chemical causing such inhibition is not known and is being investigated.

4.1.6. *Seed dormancy studies in sunflower (Helianthus annuus L.). Physiological basis of, and interaction between maternal and embryo tissues over seed dormancy.*

Student : Mr K.S. Krishnamurthy
Major Advisor : Dr R. Uma Shaanker

Summary : The aim of the study was to investigate the physiological basis of seed dormancy in sunflower and to examine the possible interactions between the maternal tissue and the embryo over the release of dormancy.

Achenes of sunflower exhibit seed dormancy ranging from 35 to 60 days. The dormancy is induced after ten days of anthesis and is lagely associated with maternal tissues such as the pericarp and the seed coat. Interestingly, the extent of imposition of dormancy by the maternal tissue was independent of the fertilization of ovule and the embryo genetic quality. However, release of dormancy was found to be dependent on the capability of the embryo to degrade the dormancy inducing factors.

The percent seeds germinated over time was clearly either positively or negatively skewed or normally distributed. Seeds of capitulum sired by a single pollen donor were characterised by a single mode in their dormancy release while those sired by multiple pollen donors, exhibited two or more modes. Further, selfed and open pollinated seeds form a given female parent differed significantly with respect to the dormancy release time.

These findings suggest that in sunflower, dormancy is imposed by the maternal parent and that maternal and embryonic tissues interact actively in breaking seed dormancy.

4.1.7. ***Physiological basis of embryo abortion in pongamia** (Derris indica **Lam and Syzygium** (Syzygium cuminii) **(L.Skeels).***

Student : Mr K.S. Krishnamurthy, Ph.D. Scholar
Major Advisor : Dr R. Uma Shaanker

Summary : Extensive embryo abortion ranging from 98% (in Syzygium) to 50% (in Pongamia) has been reported by Arathi (1990). Analyzing the proximate causes of embryo abortion in these species, she found that in Pongamia, abortion appears to be a consequence of the dominant embryo starving the subordinate, while in Syzygium, abortion is mediated by the production of a killing agent by the dominant embryo. The exact mechanism and the nature of the killing agent, however, is not yet known.

In this regard, it is proposed to investigate the following :

a. The physiological basis of starvation of the subordinate embryos by the dominant in Pongamia. This shall entail examining the effect of dominant embryos on the resource mobilizing ability of the subordinate and the possibility of the callosing of their phloem tracts.

b. The physiological basis of abortion of the subordinate emryos in Syzygium through the production of a killing agent by the dominant embryo. In this study the nature of the killing agent and the mechanism through which it causes embryo abortion will be examined.

4.2 PROJECTS

4.2.1. *Sexual selection and kin recognition mechanisms in plants.*

Summary : The proposal envisaged to study the mechanisms of male gametophytic competition, female choice and kin recognition in plants.

We have measured the intensity of male competition in plants in terms of number of pollen grains on the stigma competing for each ovule. We have also shown that male competition has played a significant role in the evolution of pollen grain to ovule ratio and floral sex ratio. For instance, male biased sex ratio in monoecious trees compared to their related herbs has been attributed to the greater opportunity for male competition in the former. We have also investigated the mechanisms with which the pollen grain pre-empt others while fertilizing the ovules and the strategies adopted by the females in inciting mate competition. The sibling interactions were studied by analysing the resource accumulation in the seeds developing in pods pollinated with pure and mixed pollen donors.

The details of the project are covered in different sections of this report.

Date of Start : April 1987
Date of Completion : September 1990
Total Cost of Project : 3,47,630/-

4.2.2. *Parent offspring interactions in plants: Mechanisms of conflict and co-operation in development and dispersal of seeds and fruits.*

Summary : The seeds and fruits in plants harbour two distinct genetic systems, namely that of the mother and of the offspring developing in close physical and temporal proximity (Uma Shaanker et al., 1988). The development of the seed and the fruit and their subsequent dispersal from the plant may not always equally increase the fitness of these genetic systems (Uma Shaanker et al., 1988; Lloyd, 1987; Ganeshaiah and Uma Shaanker, 1988). Hence, the maternal parent and the offspring may employ strategies that maximise their respective inclusive fitnesses, disregarding that to the other (Uma Shaanker et al., 1988). Thus, there might exist dynamic interactions between the mother and the offspring ranging from conflict, if their interests differ (when genetic relatedness, r is low) to co-operation if their interests coincide (when r is high).

Recently, we have recognized (Uma Shaanker et al., 1988) several situations in plants where such parent offspring interactions (POI) might be expected to operate:

a. Brood reduction in wind and animal dispersed species: where sibling rivalry to gain additional dispersal advantage causes reduction in the brood size against the maternal interest of realizing the complete brood (Uma Shaanker et al., 1988; Ganeshaiah and Uma Shaanker, 1988);

b. Seed size optimization: where offspring demand at the expense of other sibs, more resources from the maternal parent than she is selected to give (Uma Shaanker et al., 1988; Uma Shaanker and Ganeshaiah, 1988);

c. Seed dormancy: where the maternal parent imposes dormancy on the offspring and staggers their germination to overcome the density dependent mortality (Ellner, 1986). Such imposed dormancy might increase the total fitness of the mother and reduce the offspring fitness depending on the genetic relatedness between them.

This proposal is intended to provide the emperical test for these issues.

Date of start : July 1991
Date of Completion : June 1994
Total Cost of Project : 8,90,620/-

4.2.3. *Factors involved in the evolution of brood and seed size in animal dispersed plant species.*

Summary : Animal dispersal of fruit is a result of mutualistic interaction between the plants and their dispersing agents. In the process, the two partners generate selective pressures that elicit specific adaptive responses from each other (Snow, 1971; Sorenson, 1981, 1984). One such response in plants is shaping the seediness of the fruits (Mckey, 1975; Howe, 1986). However, the extent and direction in which the fruit seediness viz., seed number per fruit (brood size) and the seed size of species, are shaped depends upon the preference criteria adopted by its dispersing agents (Mckey, 1975; Howe and Vande kerckhove, 1980, 1981; Hegde et al., 1991a and b). For instance, if the animal prefers fruit with high pulp to seed ratio, selection favours fruits with few, and/or with small seed while if they prefer fruits with high absolute rewards, selection favours fruits with many or large seeds.

Besides the dispersal mode, brood and seed size are also affected by other factors such as packing cost (Ganeshaiah et al., 1986) predation (Herrara, 1984a, 1984b) and seedling establishing (Brockelman, 1975; Lloyd, 1987; Hegde et al, 1991b). In this project, it is proposed to investigate the evolution of brood and seed size in the animal dispersed species as an outcome of the interactions among all these factors.

Date Of Start	:	September 1991
Date Of Completion	:	August 1993
Total Cost Of Project	:	1,02,520/-

4.2.4. *Evolution of seed shadows and features of dispersal unit in tropical trees.*

Summary : The proposal aims to study the various spatial patterns of seed dispersal as influenced by dispersal modes in tropical trees and the mechanisms causing them. It also attempts to identify the selective forces shaping these distribution patterns. The objectives of the proposal are :

a. Identification of spatial patterns of seed dispersal of tropical tree species with different dispersal modes.

b. Identification of seed and seedling mortality factors associated with the various seed dispersal curves and dispersal modes and to isolate from these the selective forces shaping these patterns.

c. To study the cost (investment) and the benefit (due to dispersal) of several fruit features such as the number of seeds packed in fruit and design of dispersal units.

d. To study the influence of various dispersal modes on the post- dispersal seedling interaction.

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5. TRAINING
WORKSHOPS
SEMINARS

5. TRAININGS / WORKSHOPS / SEMINARS

As a part of the programme to encourage students to take up research in Evolutionary Biology and to appraise them of recent statistical techniques, our centre has been periodically arranging workshops and seminars and the same are listed below:

5.1. *Training & Workshops*

5.1.1. Workshop on Pollination Biology, Nov. 1985, Univ. Agric. Sci., Bangalore.

Speakers	Topics
1. Ganeshaiah K.N. :	A Sex ratios in plants B. Pollen dynamics
2. Umashaanker . R. :	Sexual selection in plants
3. Mallik B.A. :	A. Evolution of floral traits B. Energetics of pollination
4. Subramanya .S. :	Foraging behaviour of insect poliinations
5. Channabyre Gowda:	A. Evolution of ourcrossing mechanisms in plants B. Gene flow through pollen grains in natural and agrosystems
6. Sharathchandra H.C. :	Pollination by birds and mammals

5.1.2. Workshop on Field Techniques in Ecology and Evolution, June 1987, Nuggu, Mysore District.

5.1.3. Workshop on Field Techniques in Ecology and Evolution II, June 1988, Khadira, Uthara Kannada.

5.2 *Seminars*

5.2.1 Friday Group Seminars July 1984.

Speakers	Topics
1. Dinesh Kumar S.P.:	Endosperm balance number (EBN) hypothesis
2. Venkatesh T.V. :	Transofrmation in plants
3. Chaya B.R. :	Parasitic DNA
4. Hegde S.G. :	Bioenergetic considerations in cereal breeding
5. Belvadi V.V. :	Swollen - Thorn acacias and and their ant guests - coevolution
6. Jyothi T. :	Different methods of breaking self -incompatibility in Brassica olerocea L.
7. Uma Shaanker R. :	Phyletic size increase an analysis
8. Dasharatha Rao N.D.:	Gene transfer using irradiated pollen.
9. Murali K.S. :	Inducing variability by protoplast culture
10. Veena T. :	why an elephant feeds Bamboo - while Rabbit doesn't?
11. Balakrishna P.S. :	pollen - A rich source of variability?
12. Chidhananda S. :	Outbreeding Depression and optimal outcrossing distance.
13. Gopala Reddy P.:	Recombination in Interspecific crosses
14. Ganeshaiah K.N.:	On Mass extinctions.

5.2.2 Avalanche Seminar Series. I. Constraints in Evolution, July, 1989, Avalanche, Upper Nilgiris.

Speakers	Topics
1. Ganeshaiah K.N. :	A. is there a need to modify evolutionalry theory B. Phylogenetic tree-patttems and trends
2. UmaShaanker.R :	Developmental constraints in evolution
3. Veena .T :	Panglosian paradigm
4. Hegde S.G. :	Punctuated equilibrium
5. Chandrashekara. K:	Optimising behaviour in evolutionary theory
6. Kumar A.R.V. :	Constraints for sexual selection in emphids
7. Subramanya S. :	Use of economic models in understanding foraging behaviours
8. Prabhakar :	Natural History of Nilgiris
9. Mallik.B.A. :	Prey and patch models
10. Radhamani.T.R. :	Lek formation in bats
11. Vasudeva R. :	Universal aspects of biological evolution.
12. Arun V. :	Neutral mutation theory

5.2.3. Friday group symposium on "Trans-oceanic contact between the old and new worlds and cultivation of maize in India", December, 1989, Somanathpur, Mysore District.

5.2.4. Avalanche Seminar Series. II. Learnming and Memory in animals, June, 1991, Heggadi Halli near Nandi Hills, Bangalore District.

Speakers		Topics
1. Veena T.	:	Orientation in foraging animals
2. Gadagkar R.	:	Cognitive maps in animals
3. UmaShanker R.	:	Perception of shape in insects
4. Sinha A.	:	Concept of time and number in animal cognition
5. Subramnaya S.	:	Mental maps in the Barn Owl
6. Radhamani T.R.	:	Echolocation in bats
7. Deviprasad K.V.	:	Do elephants remember ?
8. Walve M.G.	:	Why human Species has less predators?
9. Ganeshaiah K.N.	:	Self - organised behaviour in social insects
10. UmaShaanker R.	:	Decisions - making in uncertain Environments
11. Gadagkar R.	:	Memory in animals
12. Ganeshaiah K.G.	:	Search strategies of foraging animals
13. Hegde S.R.	:	Genetics of learing and memory
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6. PUBLICATIONS FROM THE CENTRE

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